



## Semi-natural habitat complexity affects abundance and movement of natural enemies in organic olive orchards

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### ABSTRACT

Olive orchards have been shown to be able to improve the abundance of natural enemies due to the establishment of adjacent vegetation and ground cover in recent years. Yet evidence regarding the positive effects that such semi-natural habitats provide to the presence and movement of the trophic guilds of the arthropod community is lacking. In this study we assess the effects that plants, both as individual species and as semi-natural habitat assemblages, have on the abundance, presence, and movement of the arthropod community in organic olive orchards. We collected 97 families of arthropods from the canopy of olive trees and the foliage of plants in the ground cover and adjacent vegetation. We analysed the data in relation to habitat complexity. Our results show that the abundance of natural enemies is higher in areas with more complex semi-natural habitats. Parasitoids were able to colonize the olive trees, irrespective of the area or type of vegetation. Predators and parasitoids occurred in the ground cover and adjacent vegetation, but not in the orchard. The adjacent vegetation mainly acted as an important sink for natural enemies when the ground cover withered in June–July, and thus, ground cover and adjacent vegetation may serve as a source of parasitoids and predators for colonizing olive trees. Overall, the density of the natural enemies in organic olive orchards is better enhanced by complex stands of ground cover and natural adjacent vegetation, which gives support to the complex-habitat hypothesis.

### 1. Introduction

Agroecological theory suggests that semi-natural habitats provide food and shelter to natural enemies of insect pests (Altieri, 1999, 2000; Tscharntke et al., 2012, 2016; Wan et al., 2018a). It has been suggested that some natural enemies (i.e., arthropods) respond negatively to the presence of semi-natural habitats (Karp et al., 2018), which is a problem in conservation biological control. A positive or negative response shown by an organism to a nearby habitat could be driven by the structure of such a habitat (Laurance, 2007; López-Barrera et al., 2007; Broadbent et al., 2008; Balmford et al., 2012; Álvarez et al., 2016, 2017; Wan et al., 2019). Indeed, arthropod richness responds negatively to fragmentation and disturbance (Hogsden and Hutchinson, 2004; Dallimer et al., 2012) but arthropod abundance has complex and controversial patterns (Ries and Sisk, 2004), which are conditioned by factors related to landscape complexity (Rusch et al., 2010; Tscharntke et al., 2012, 2016). Bianchi et al. (2006) proposed a hypothesis relating the presence of semi-natural habitats with an abundance of natural

enemies in an agroecosystem. This hypothesis (hereafter referred to as the complex-habitat hypothesis) suggests that complex low-fragmented landscapes with a high proportion of semi-natural habitats boost the populations of natural enemies within agroecosystems (Bianchi et al., 2006; Rusch et al., 2010).

In perennial crops, controversial results have been reported about the effects of semi-natural habitats on the abundance of natural enemies. For example, some studies have reported an increase in abundance (Danne et al., 2010; Silva et al., 2010; Karp et al., 2018; Wan et al., 2014a, 2014b, 2018b), whereas others have reported no effects (Costello and Daane, 1998; Bone et al., 2009; Karp et al., 2018). In olive orchards recent studies have suggested an improvement in the abundance of natural enemies due to the presence of ground cover and adjacent vegetation in and around orchards (Ruano et al., 2004; Paredes et al., 2013a; Gkisakis et al., 2016, 2018). Indeed, landscape structure and the management of the ground cover positively affect the abundance and variability of natural enemies (Gkisakis et al., 2016; Villa et al., 2016). However, the synergy between both habitats may have an

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important role in predicting the type of organisms that can be found in an olive tree (Paredes et al., 2013a, 2013b). Thus, an increase in natural enemy abundance would reduce populations of herbivore insects.

Despite the efforts of different authors to assess the effects of ground cover and adjacent vegetation on natural enemies and olive pests (Paredes et al., 2013a; Jiménez-Muñoz et al., 2017; Manjón Cabezas Córdoba et al., 2017; Villa et al., 2016a; 2016b; Porcel et al., 2017; Gkisakis et al., 2016, 2018), to the best of our knowledge there is no study that has focussed on the abundance, presence, and movement of the overall arthropod community in both habitats and their interaction with olive orchards. This point of view is of great importance because, unlike insect pests, natural enemies require a non-crop environment at one or more stages of their life cycle (Keller and Häni, 2000; Rusch et al., 2010). Furthermore, spill over is based on the ability of organisms to move between vegetations, which is driven by the trophic level (i.e., organisms at higher trophic levels operate at a larger spatial scale, Holt, 1996) and body size (Tscharntke et al., 2005).

Empirical data are needed to understand the interaction amongst ground cover, adjacent vegetation, and all types of olive orchards. However, this study just focuses on organic olive orchards. A decision motivated by (1) the need to understand the system in the most natural conditions, (2) the increase in modern demand for organic food, and (3) the policies currently being implemented with the aim of restoring native habitats (e.g., the European Union, IOBC, 2012), which encourages producers to start managing olive orchards in an organic manner (Alonso Mielgo et al., 2001; Torres-Miralles et al., 2017). The aim of this study is to establish the effects that plants as individual species and as habitat assemblages i.e., ground cover and adjacent

vegetation, have on the abundance, presence, and movement of the arthropod community, especially the guilds of natural enemies, in organically managed olive orchards.

## 2. Materials and methods

### 2.1. Study area

The study was conducted in organic olive orchards (186.45 ha, Fig. 1), located in the province of Granada, southern Spain. Olive orchards were selected based on (1) the presence of patches of adjacent vegetation, and (2) the use of mowing techniques and no herbicides, and thus maintaining the ground cover for at least three consecutive years (Fig. S1). Four patches of adjacent vegetation (study areas) were found amongst three olive orchards: three patches in the locality of Piñar (37°24'N and 3°29'W) and one in the locality of Deifontes (37°19'N and 3°34'W). *Bacillus thuringiensis* was sprayed in randomly selected sections (but not all the area) in July. This was used as a preventive pest control for the carpophagous generation of *P. oleae* (larvae) in the orchards of Piñar. Climatic conditions for the hydrological year of 2014–2015 in the region were: 16.0 °C mean annual temperature, 31.9 °C–15.9 °C mean maximum and minimum temperatures from May to July, and 429.6 mm mean annual precipitation. In this area the main insect pest that damages olives is the olive moth, *Prays oleae* Bern (Lepidoptera: Plutellidae) (Red de alerta e Información fitosanitaria de Andalucía (RAIF, 2018), which is widely distributed in the circum-Mediterranean region (Tzanakakis, 2006).

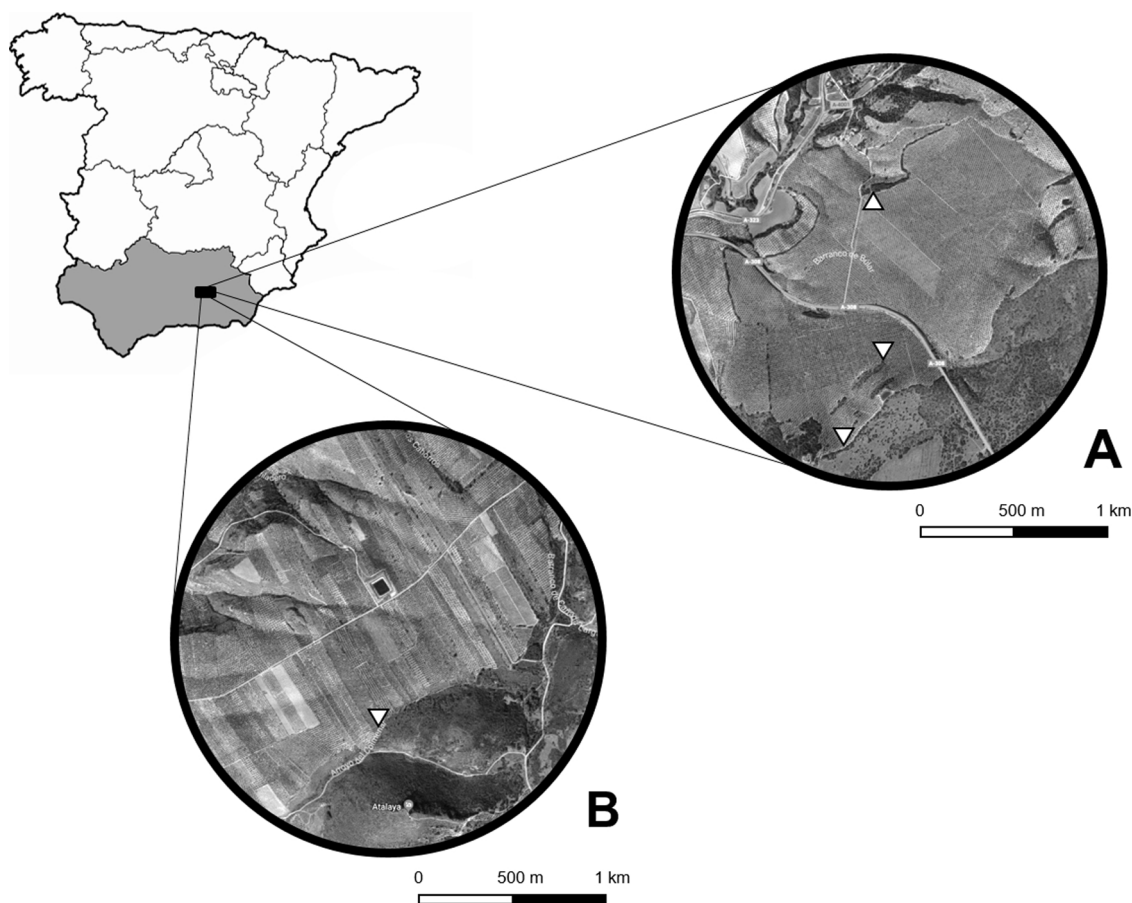


Fig. 1. Location of the study areas in southern Spain. Distribution of the patches of adjacent vegetation (triangles) in Piñar (A) and Deifontes (B).

**Table 1**

Plant species composition and structure in the four study areas of organic olive orchards: Deifontes (DEI), Piñar 1 (PI-1), Piñar 2 (PI-2), and Piñar 3 (PI-3). Plant species in adjacent vegetation: *C. albidus* (Ca), *P. dulcis* (Pd), *Q. rotundifolia* (Qr), *R. sphaerocarpa* (Rs), *R. officinalis* (Ro), *T. mastichina* (Tm), *T. gracilis* (Tzg), *U. parviflorus* (Up). Plant species in ground cover: *A. radiatus* (Ar), *C. melitenses* (Cm), *D. catholica* (Dc), *E. cicutarium* (Ec), *L. longirostris* (Ll), *S. vulgaris* (Sv).

Plant species composition			
Area	Adjacent vegetation	Ground cover	Patch structure
DEI	Qr - Rs - Ro - Tzg - Up - Ca - Pd - Tm	Ll - Dc - Cm - Ec - Sv	Dominated by Qr and Pd, others gathered in one cluster
PI-1	Qr - Rs - Ro - Tzg - Up	Ll - Dc - Ar	Gathered into clusters
PI-2	Qr - Rs - Ro - Tzg - Up	Ll - Dc	All scattered
PI-3	Qr - Rs	Ll	Dominated by Qr

## 2.2. Plant composition and structure

Eight plant species were abundant in the adjacent vegetation: *Cistus albidus* L., *Prunus dulcis* (Mill.) D. A. Webb, *Quercus rotundifolia* Lam., *Retama sphaerocarpa* (L.) Boiss., *Rosmarinus officinalis* L., *Thymus mastichina* (L.) L., *Thymus zygis gracilis* (Boiss.) R. Morales and *Ulex parviflorus* Pourr. Six species of herbaceous plants were found in the blossom period in the ground cover: *Anacyclus radiatus* Loisel, *Centaurea melitenses* L., *Diploaxis catholica* (L.) DC., *Erodium cicutarium* (L.) L'Hér, *Leontodon longirostris* (Finch & P.D. Sell) Talavera and *Senecio vulgaris* L.

The structure of the vegetation within the patches showed differences. In Piñar 1 (PI-1) and Piñar 2 (PI-2) the structure was similar, plants were distributed and scattered all over the patches, but the plants in PI-1 were gathered in clusters of vegetation. Conversely, in Deifontes (DEI) most of the patch was occupied by two tree species and the rest of the species were gathered in one cluster of vegetation. Finally, Piñar 3 (PI-3) was occupied mostly by one species. Table 1 summarizes plant species composition and the structure of the semi-natural habitats in the study areas.

The differences in species composition in both adjacent vegetation and ground cover, and the structure of the adjacent vegetation (Table 1) were used to establish a qualitative gradient of complexity. We arranged the study areas from most to least complex as: PI-2, PI-1, DEI and PI-3.

## 2.3. Specimen collection and sampling design

We focussed our efforts on collecting samples of arthropods (1) in the most abundant and recognizable (blossom) plant species within adjacent vegetation and ground cover, and (2) in the canopy of the olive trees. Our experimental unit (sample) was a suction plot that was a 30 s-suction in a 50 × 50 cm surface of plant foliage. We used a modified vacuum device CDC Backpack Aspirator G855 (John W. Hock Company, Gainesville, FL, USA). This method allows us to standardize sampling amongst different types of plants (i.e., herbaceous, shrubs, and trees).

Samples in this study were collected, weather permitting (once a month) from May to July 2015, which are the months of highest arthropod abundance (Ruano et al., 2004; Santos et al., 2007). We collected 20 randomly distributed samples per plant species, depending on plant species availability (Table 1). In addition, in order to test edge effects between adjacent vegetation and the olive trees, we collected 40 randomly distributed samples in the olive trees per patch of adjacent vegetation. These samples were taken in trees near to the adjacent vegetation (edge trees) and trees far from the adjacent vegetation near to the centre of the orchard (inner trees) (20 samples per section). The edge trees had a separation of 550 m from the inner trees (approximately). The samples were stored individually and maintained at

−20 °C until the specimens were classified. The arthropods were identified to family level, unless otherwise specified, and classified by trophic guilds i.e., omnivore, parasitoid, predator (natural enemies) and specialist olive pests. The families that were identified as neither natural enemies nor pests were gathered together in a group named neutral arthropods (Wan et al., 2014a). Guild classification was based on literature data (see Appendix A in Supporting information). Raw sample data was used to conduct analyses.

## 2.4. Differences in arthropod abundance

Arthropod abundance was analysed by comparing the study areas and the types of vegetation, for which several generalised linear models (GLMs) were constructed using “quasi-likelihood” with Poisson-like assumptions (quasi-Poisson) tendency (for justification on this approach see Ver Hoef and Boveng, 2007). Firstly, to compare (1) overall arthropod abundance, (2) total abundance of natural enemies (i.e., omnivores, parasitoids, and predators together), and (3) abundance of omnivores, parasitoids, and predators, we fitted models including abundance as the dependent variable and type of vegetation and study area as factors. Secondly, to compare the total abundance of natural enemies amongst plant species, we fitted a model including abundance as the dependent variable and the plant species and study area as factors. In all the GLMs the sampling date was controlled using the month as a factor. Further differences between the groups in each model were tested using analyses of deviance and the Tukey post hoc (contrasts) test. The R software v 3.5.0 (R Developmental Core Team, 2018) was used to compute all the analyses. Tukey test was computed using the “multcomp” package (Hothorn et al., 2008).

## 2.5. Arthropod presence and movement

To understand and visualize differences in abundance amongst the study areas and the types of vegetation, multivariate techniques were used. Family level abundance was pulled together by the type of vegetation per month in each study area, and then it was subjected to principal component analysis (PCA) in R software v 3.5.0 (R Developmental Core Team, 2018). We analysed the interrelation between the abundance of all the trophic guilds and the type of vegetation in each study area (per month), by using a correspondence analysis (CA) approach (Greenacre, 2013). CA was used to describe the movement of arthropods across the vegetation by direct effects of abundance on ordination. This was achieved by introducing categorical data of presence in each type of vegetation and ID data of each trophic guild. Then, abundance scores were used to weight the data. One of the goals of CA is to describe the relationships between two nominal variables in a low-dimensional space, whilst describing the relationships between the categories for each variable. CA as an eigenvector technique also weights sites and organisms (using Chi-square metrics) by their totals in eigen analysis (Legendre and Gallagher, 2001; Greenacre, 2013). CA was carried out in SPSS software v 19 (IBM Corp., 2010).

## 2.6. Distance with adjacent vegetation

We compared the abundance of each guild of natural enemies (i.e., omnivores, parasitoids, and predators) between inner and edge (olive) trees in the four study areas. A Wilcoxon-Mann-Whitney rank sum test was computed, using the data of the three months together, in R software v 3.5.0 (R Developmental Core Team, 2018).

## 3. Results

A total of 7381 individuals were collected in 1856 suction samples. The arthropods were comprised in 12 orders: Araneae, Blattodea, Coleoptera, Diptera, Dermaptera, Hemiptera, Hymenoptera, Lepidoptera, Mantodea, Neuroptera, Phasmida, Raphidioptera, and

**Table 2**

Relative abundance and trophic guilds of all the families of arthropods ( $n = 97$ ) identified in organic olive orchards and semi-natural habitats.

Name		Guild	Relative Abundance (%)
Arachnida			
Araneae	Amaurobiidae	Predator	0,041
	Araneidae	Predator	0,352
	Dyctinidae	Predator	0,027
	Linyphiidae	Predator	0,176
	Mimetidae	Predator	0,014
	Oxyopidae	Predator	1,016
	Philodromidae	Predator	0,257
	Salticidae	Predator	0,379
	Sicariidae	Predator	0,014
	Thomisidae	Predator	2,940
	Uloboridae	Predator	0,339
	Zodariidae	Predator	0,054
Insecta			
Blattodea	Blattellidae	Neutral arthropod	0,108
Coleoptera	Alleculidae	Neutral arthropod	0,095
	Anthicidae	Neutral arthropod	0,068
	Apionidae	Neutral arthropod	0,081
	Cantharidae	Predator	0,041
	Catopidae	Neutral arthropod	0,068
	Chrysomelidae	Neutral arthropod	0,975
	Cleridae	Predator	0,041
	Coccinellidae	Predator	0,921
	Curculionidae	Neutral arthropod	1,612
	Dasytidae	Predator	0,135
	Dermeestidae	Neutral arthropod	0,041
	Elateridae	Predator	0,014
	Malachiidae	Predator	0,027
	Monotomidae	Neutral arthropod	0,014
	Mycetophagidae	Neutral arthropod	0,014
	Nitidulidae	Neutral arthropod	0,027
	Phalacridae	Neutral arthropod	0,718
	Ptinidae	Neutral arthropod	0,014
	Scarabaeidae	Neutral arthropod	0,014
	Staphylinidae	Predator	0,054
Dermaptera	Forficulidae	Omnivore	0,014
Diptera	Agromyzidae	Neutral arthropod	0,027
	Asilidae	Predator	0,014
	Bibionidae	Neutral arthropod	0,014
	Bombyliidae	Neutral arthropod	0,108
	Calliphoridae	Neutral arthropod	0,014
	Camillidae	Neutral arthropod	0,135
	Cecidomyiidae	Neutral arthropod	0,217
	Ceratopogonidae	Neutral arthropod	0,014
	Chamaemyiidae	Predator	0,014
	Chironomidae	Neutral arthropod	0,054
	Chloropidae	Neutral arthropod	0,230
	Dolichopodidae	Predator	0,163
	Empididae	Neutral arthropod	0,095
	Heleomyzidae	Neutral arthropod	0,014
	Limoniidae	Neutral arthropod	0,027
	Muscidae	Neutral arthropod	0,068
	Opomyzidae	Neutral arthropod	0,014
	Phoridae	Neutral arthropod	0,014
	Sciaridae	Neutral arthropod	0,095
	Tephritidae	Neutral arthropod	0,271
Hemiptera	Anthracoridae	Predator	0,122
	Aphididae	Neutral arthropod	18,493
	Berytidae	Neutral arthropod	0,122
	Coccidae	Neutral arthropod	0,312
	Cydnidae	Neutral arthropod	0,014
	Fulgoromorpha	Neutral arthropod	13,887
	Geocoridae	Predator	0,027
	Lygaeidae	Predator	0,610
		(facultative)	
	Miridae	Predator	3,943
	Nabidae	Predator	0,027
	Pentatomidae	Neutral arthropod	0,542
	Psyllidae	Neutral arthropod	14,564
	Rhopalidae	Neutral arthropod	0,339
	Tingidae	Neutral arthropod	0,244

**Table 2 (continued)**

Name		Guild	Relative Abundance (%)
Hymenoptera	Aphelinidae	Neutral arthropod	0,054
	Apidae	Neutral arthropod	0,447
	Bethylidae	Parasitoid	0,149
	Braconidae	Parasitoid	0,528
	Ceraphronidae	Neutral arthropod	0,014
	Chrysididae	Parasitoid	0,014
	Cynipidae	Neutral arthropod	0,027
	Diapriidae	Parasitoid	0,027
	Elasmidae	Parasitoid	0,095
	Encyrtidae	Parasitoid	0,854
	Eulophidae	Parasitoid	0,122
	Eupelmidae	Parasitoid	0,027
	Eurytomidae	Parasitoid	0,041
	Formicidae	Omnivore	22,246
	Ichneumonidae	Parasitoid	0,054
	Mymaridae	Parasitoid	0,068
	Platygastridae	Parasitoid	0,041
	Pompilidae	Neutral arthropod	0,014
	Pteromalidae	Parasitoid	0,406
	Scelionidae	Parasitoid	0,528
Lepidoptera	Plutellidae	Neutral arthropod	0,406
Mantodea	Mantidae	Predator	0,054
Neuroptera	Chrysopidae	Predator	0,434
	Coniopterygidae	Predator	0,027
Phasmatodea	Phasmatidae	Neutral arthropod	0,014
Raphidioptera	Raphidiidae	Predator	0,027
Thysanoptera	Aeolothripidae	Predator	2,642
	Phlaeothripidae	Neutral arthropod	1,057
	Thripidae	Neutral arthropod	4,037

Thysanoptera. Table 2 summarizes information regarding the relative abundance and trophic guild for each arthropod family. Overall, 97 families were identified. Then, 49 families were classified as natural enemies in three trophic guilds: 2 omnivores, 15 parasitoids, and 32 predators. 2 families were identified as specialist pests of olive orchards, the rest of the families were grouped as neutral arthropods.

### 3.1. Differences in arthropod abundance

#### 3.1.1. Areas and vegetation

The arthropod abundance differed amongst study areas and showed a positive relation with the level of complexity. The study area had a significant effect on the overall abundance ( $F_{3,1850} = 8.464$ ,  $p = 0.001$ ) (Table 3). PI-1 and PI-2 had higher abundance than PI-3 (Tukey test,  $p = 0.001$ ) and DEI ( $p < 0.004$ ) but there were no differences between PI-1 and PI-2 ( $p = 0.999$ ) and between PI-3 and DEI ( $p = 0.245$ ). Secondly, the study area had a significant effect on the abundance of natural enemies (total abundance:  $F_{3,1850} = 26.743$ ,  $p = 0.001$ ), which was similar to the pattern of overall abundance (Fig. 2). However, when separated by guild, this pattern was only significant for omnivores and predators (Fig. 2). Indeed, omnivore abundance showed significant differences ( $F_{3,1850} = 27.946$ ,  $p = 0.001$ ). PI-2 had higher abundance than the rest of the areas (DEI and PI-3,  $p = 0.001$ ; PI-1,  $p = 0.002$ ) but PI-1 had higher abundance than DEI ( $p = 0.001$ ). There were no differences between PI-3 and DEI ( $p = 0.86$ ) and between PI-1 and PI-3 ( $p = 0.072$ ). Likewise, predator abundance showed significant differences ( $F_{3,1850} = 3.924$ ,  $p = 0.008$ ). PI-1 had higher abundance than PI-3 ( $p = 0.023$ ) and DEI ( $p = 0.031$ ) but there were no differences for the rest of the combinations. Conversely, parasitoid abundance was not significantly different amongst the study areas ( $F_{3,1850} = 1.341$ ,  $p = 0.259$ ).

On the other hand, the type of vegetation had a significant effect on the overall abundance ( $F_{2,1853} = 60.075$ ,  $p = 0.001$ ) (Table 3). Ground cover had higher arthropod abundance than adjacent vegetation (Tukey test:  $p = 0.001$ ) and olive trees ( $p = 0.001$ ) but there were no

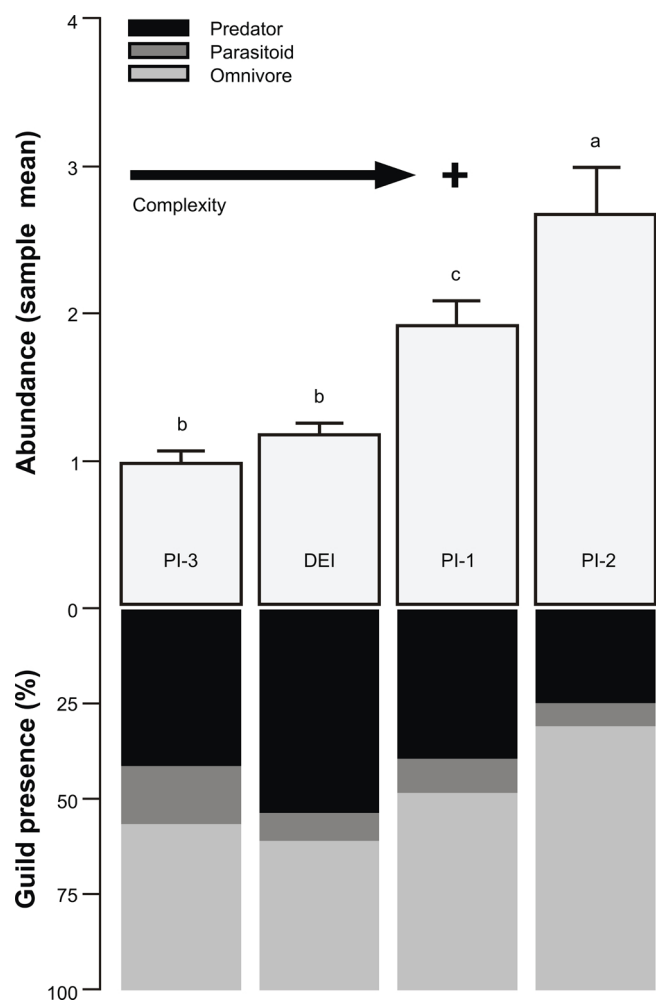


Fig. 2. Overall abundance of natural enemies amongst study areas. Mean sample ( $n = 1856$ ), standard deviation, and percentage of guild presence in each study area: Deifontes (DEI), Piñar 1 (PI-1), Piñar 2 (PI-2), and Piñar 3 (PI-3). Study areas are arranged from most to least complex.

Table 3

Descriptive statistics of overall arthropod abundance compared in GLM analyses amongst types of vegetation and study areas: Deifontes (DEI), Piñar 1 (PI-1), Piñar 2 (PI-2), and Piñar 3 (PI-3).

	Mean	SD
DEI	3.74	8.72
PI-1	4.73	12.65
PI-2	5.11	9.83
PI-3	2.25	2.48
Adjacent vegetation	3.09	10.03
Ground cover	9.45	12.34
Olive	3.20	3.42

Table 4

Descriptive statistics of abundance (Mean  $\pm$  SD) of natural enemy (NE) guilds compared in GLM analyses amongst types of vegetation.

Type	Type of vegetation		
	Adjacent	Ground cover	Olive
NE Total	1.57 $\pm$ 5.00	3.75 $\pm$ 5.49	0.68 $\pm$ 1.13
Omnivore	1.01 $\pm$ 4.61	1.42 $\pm$ 4.23	0.26 $\pm$ 0.69
Parasitoid	0.06 $\pm$ 0.41	0.27 $\pm$ 0.61	0.14 $\pm$ 0.46
Predator	0.39 $\pm$ 1.18	2.05 $\pm$ 3.46	0.27 $\pm$ 0.67

differences between adjacent vegetation and olive trees ( $p = 0.589$ ). The type of vegetation also had a significant effect on the abundance of natural enemies ( $F_{2,1853} = 70.737$ ,  $p = 0.001$ ) (Table 4). When separated by guild, omnivore abundance showed significant differences ( $F_{2,1853} = 25.149$ ,  $p = 0.001$ ). Olive trees had lower omnivore abundance than the adjacent vegetation (Tukey test:  $p = 0.001$ ) and ground cover ( $p = 0.001$ ) but there were no differences between adjacent vegetation and ground cover ( $p = 0.154$ ). Significant differences were found though in the same pattern for both parasitoid abundance ( $F_{2,1853} = 11.672$ ,  $p = 0.001$ ) and predator abundance ( $F_{2,1853} = 105.615$ ,  $p = 0.001$ ). Ground cover had a higher abundance of parasitoids and predators than the adjacent vegetation ( $p = 0.001$ ) and the olive trees ( $p < 0.027$ ) but there were no differences between the adjacent vegetation and the olive trees (parasitoids,  $p = 0.047$ ; predators,  $p = 0.138$ ).

### 3.1.2. Plant species

Plant species had a significant effect on the abundance of natural enemies (total abundance:  $F_{14,1841} = 16.428$ ,  $p = 0.001$ ) (Fig. 3). Firstly, *O. europaea* had a lower abundance than the shrubs *C. albidus*, *R. officinalis*, *R. sphaerocarpa*, *T. mastichina*, and *T. zygis gracilis* and the herbaceous plants *A. radiatus*, *D. catholica*, *L. longirostris*, and *S. vulgaris* (Tukey test:  $p < 0.037$ ). These herbaceous plants had the highest abundance of natural enemies. Secondly, *Q. rotundifolia* had a lower abundance than *A. radiatus*, *C. albidus*, *D. catholica*, *L. longirostris*, *R. sphaerocarpa*, *S. vulgaris*, and *T. z. gacillis* ( $p < 0.018$ ). On the other hand, *L. longirostris* had a higher abundance than *P. dulcis*, *R. officinalis*, *R. sphaerocarpa*, *T. z. gracilis*, and *U. parviflorus* ( $p < 0.020$ ). Finally, *A. radiatus* and *D. catholica* had a higher abundance than *R. officinalis* and *U. parviflorus* ( $p = 0.001$ ). Overall, almost all the species in adjacent vegetation and ground cover had high abundances of the three natural enemies guilds compared with those found in the olive trees. Four species of herbaceous plants contributed to the increase of predator abundance in ground cover more than the other guilds (Fig. 3). Moreover, all the shrub plants contributed to the increase of omnivore abundance in adjacent vegetation (Fig. 3).

### 3.2. Arthropod presence and movement

The PCA showed that the difference between the study areas was explained by the variance of overall arthropod abundance in the ground cover of DEI and PI-1, and the adjacent vegetation of PI-2 (Fig. 4). 49.31% of the variance was explained by PC1, and 39.40% by PC2. The families that showed the highest loadings in variance were Aphididae, Formicidae, Fulgoromorpha, Miridae, Psyllidae, and Thripidae. Accordingly, Aphididae, Fulgoromorpha, Miridae, and Thripidae contributed mainly to the variance of ground cover, Formicidae to adjacent vegetation and Psyllidae to olive trees (Fig. 4).

Fig. 5 shows the results of 12 correspondence analyses (CAs) separated by months for each study area. It represents a pattern of increase or decrease in abundance (that can be interpreted as movement) in the three types of vegetation, which includes all the guilds of arthropods in a low dimensional space. This separation was made in order to simplify the tendencies in the data. Overall, the CAs showed that dimension one explained almost the total of the inertia in all the study areas and months. The CAs showed differences by month and study area. The number of families was higher in May for most of the areas, except for DEI, which had a higher number of families in June. On the other hand, the correspondence between guilds and the types of vegetation presented some tendencies. In May, omnivores were related with adjacent vegetation, and the other guilds were linked with ground cover (except parasitoids in DEI). In June parasitoids were mostly present in the olive trees, and the predators, omnivores and neutrals in adjacent vegetation (except predators in PI-3 and neutrals in DEI). In July most predators, neutrals, and parasitoids were found in the adjacent vegetation (except parasitoids in PI-3) but the omnivores showed no pattern. Finally, in the

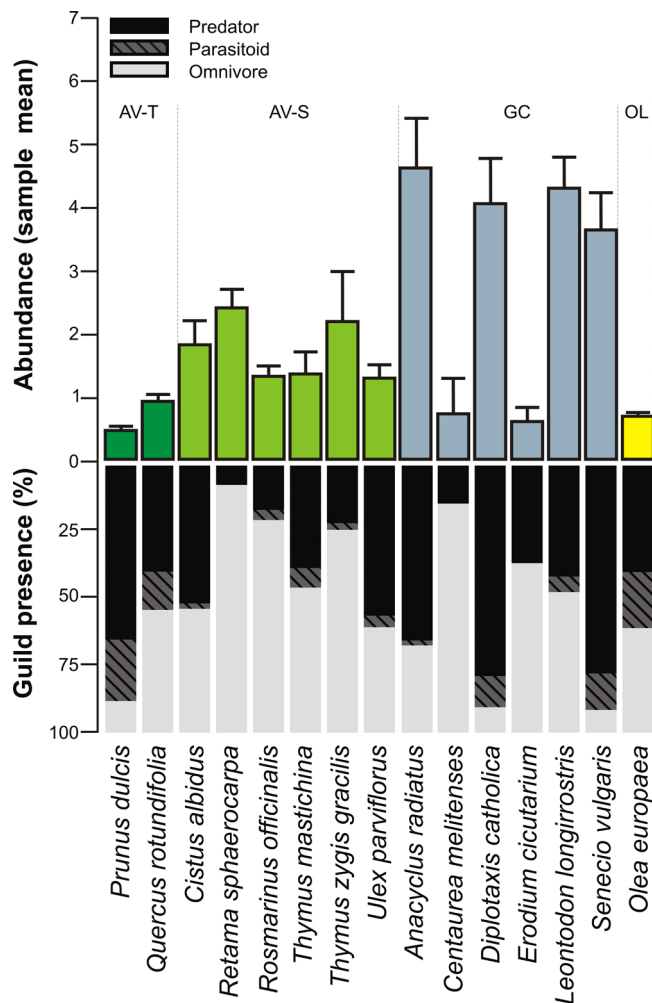


Fig. 3. Overall abundance of natural enemies amongst plant species. Mean sample ( $n = 1856$ ), standard deviation, and percentage of guild presence in each plant. Plants are arranged by type of vegetation: ground cover (GC), olive orchard (OL), and adjacent vegetation was separated for more detail in trees (AV-T) and shrubs (AV-S).

three months studied the pests were only related with olive trees. Moreover, in almost all the areas the ground cover started to wither in June, and thus by July the ground cover was almost empty of natural enemies. Therefore, the guilds moved across the different types of vegetation. For example (1) the predators moved from ground cover to adjacent vegetation from May to June, with the possibility of moving to the olive trees when the ground cover withered; (2) the omnivores moved from the adjacent vegetation to the ground cover and olive trees in July; and (3) the parasitoids moved from the ground cover to the olive trees from May to June when the ground cover withered (Fig. 6).

### 3.3. Distance with adjacent vegetation

Overall, the abundance of natural enemies within an olive tree was not related with the distance of the trees to the adjacent vegetation. However, only omnivores showed higher abundance within the canopy of the inner trees rather than the edge trees in PI-1 and PI-2 (Wilcoxon-Mahn-Whitney:  $W = 1505$ ,  $p = 0.005$ ;  $W = 1385$ ,  $p = 0.005$ , respectively).

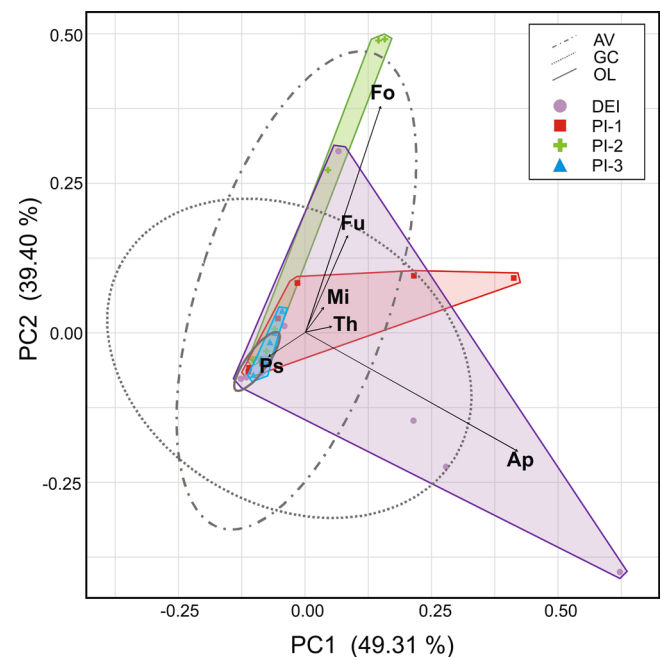


Fig. 4. Principal component analysis. Data clustered by study areas: Deifontes (DEI), Piñar 1 (PI-1), Piñar 2 (PI-2), and Piñar 3 (PI-3). The calculated ellipses assume a multivariate  $t$  distribution and represent the type of vegetation: adjacent vegetation (AV), ground cover (GC), and olive orchards (OL). Arthropod families: Aphididae (Ap), Formicidae (Fo), Fulgoromorpha (Fu), Miridae (Mi), and Thripidae (Th).

## 4. Discussion

### 4.1. Habitat complexity

The presence of natural enemies in organic olive orchards, and their relationship with adjacent vegetation and ground cover, correlates with habitat complexity. There is more abundance when semi-natural habitats have high numbers of plant species and plants are arranged and dispersed across the entire area (Fig. 6). This was reflected in the predators and omnivores (Fig. 2). It has been shown that the structure of non-crop vegetation has a direct effect on an enemy's preference for a habitat, specifically, hedgerow plots with mixed plant species have a greater presence of natural enemies than plots with a single species (Campbell et al., 2012; Miñarro and Prida, 2013; Morandin et al., 2014; Cotes et al., 2018). This tendency has also been seen in the ground cover of olive orchards (Gómez et al., 2018). Nonetheless, the difference in plant species composition and structure between our study areas seemed to have no effect on parasitoid abundance (Fig. 6). This could be explained, firstly, by the fact that our sample method is not the optimum for flying hymenopterans, and secondly, because such insects have a wide range of movement (Rusch et al., 2010).

### 4.2. Relationship with vegetation

Overall, abundance is affected by the type of vegetation. Most plant species had a higher abundance of natural enemies than the olive trees, although each trophic guild had a specific relationship with a type of vegetation. For example, it is known that parasitoids and some predators greatly benefit from the presence of sources of pollen and nectar inside crops (Wäckers, 2001; Berndt et al., 2006; Winkler et al., 2006; Rusch et al., 2010). In olive orchards this tendency is due to the

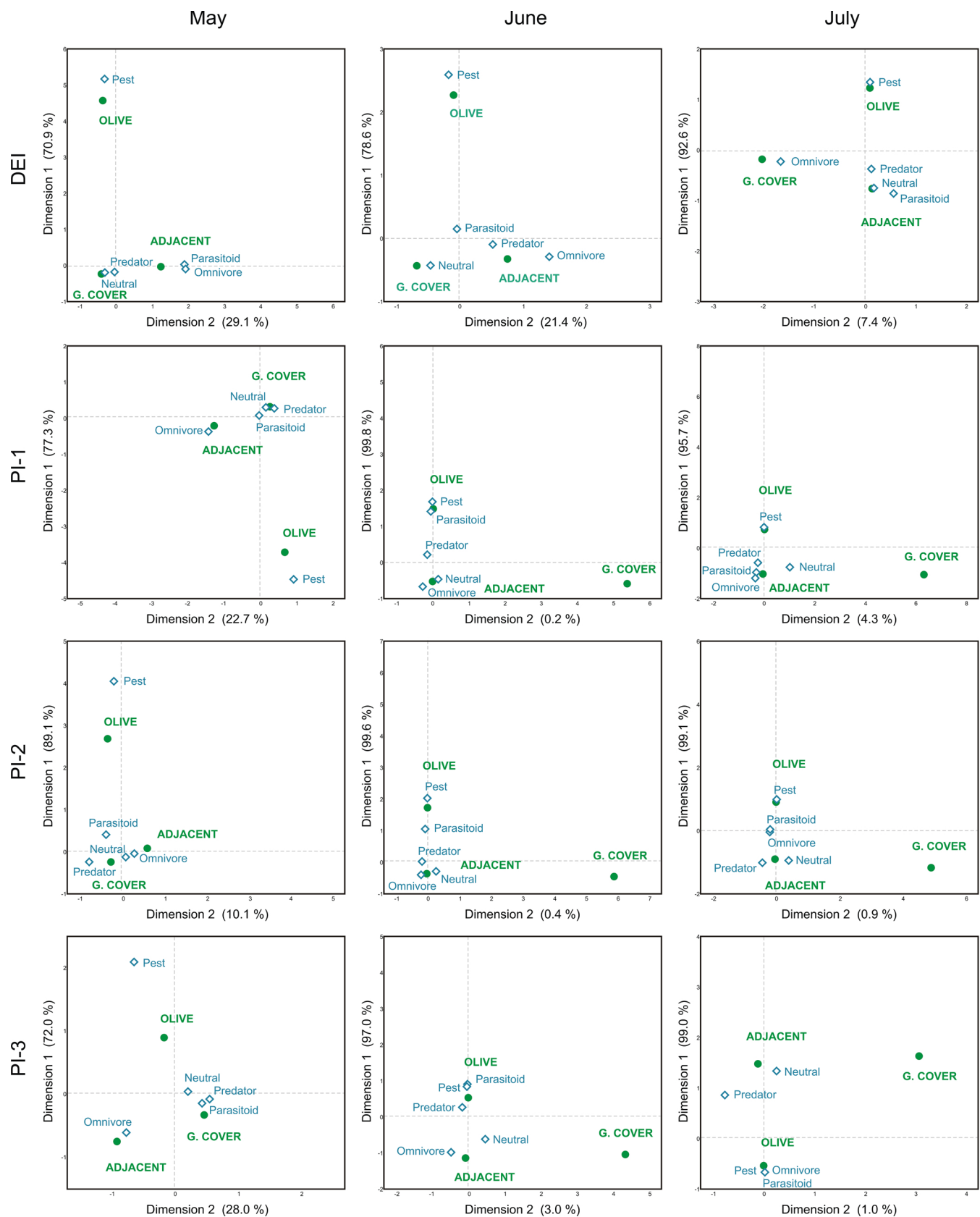
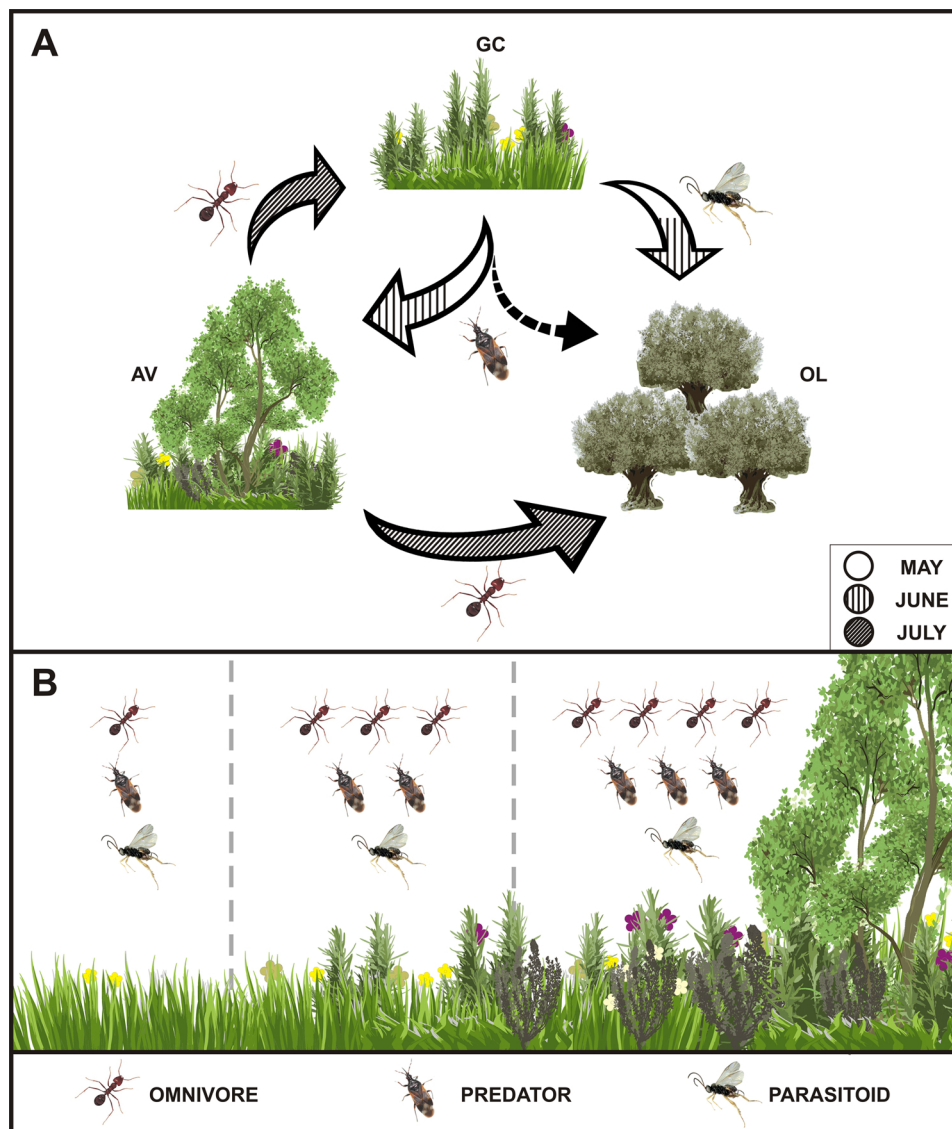


Fig. 5. Correspondence analyses. Rhomboids represent overall abundances separated by trophic guilds, circles represent each type of vegetation. Data is presented by month and study area: Deifontes (DEI), Piñar 1 (PI-1), Piñar 2 (PI-2), and Piñar 3 (PI-3).



**Fig. 6.** Graphic representation of movement of natural enemies (A) and abundance response to habitat complexity (B). Movement across adjacent vegetation (AV), ground cover (GC), and olive orchards (OL). Arrows indicate the direction of the movement and the plot inside the arrows shows the month in which the movement happens. A dotted arrow indicates the possibility of movement.

relationship between floral architecture and insect morphology (Nave et al., 2016), which in some cases increases the parasitism rate (Villa et al., 2016). This could explain why, in our case, the herbaceous plants in the ground cover maintained the presence (percentage) and abundance of parasitoids (Fig. 3). Paredes et al. (2013a) showed, by modelling, that adjacent vegetation positively affected the abundance of parasitoids within the olive orchard, but also that parasitoids had a stronger dependence on herbaceous habitats (i.e., ground cover). In their study, when such habitats were missing the predicted abundance was zero. This pattern is in accordance with our results. Furthermore, Paredes et al. (2013a) showed that parasitoid abundance dropped in July, which matches with the tendencies shown by our CAs in the same month.

It has been reported that alternative prey for predators is of great importance when the enhancement of biological control in agroecosystems is desired (Rusch et al., 2010). For example, some species of predator coccinellids are affected by prey availability in non-crop habitats when their primary source of food is not present, becoming

increasingly dependent on alternative sources (Bianchi and van der Werf, 2004; Rand et al., 2006), which can, in some cases, increase their fitness (Rusch et al., 2010). However, the dependence of a natural enemy on alternative prey is greater for a generalist predator than for a specialist predator (Rusch et al., 2010). In our study the predator families were mostly generalists which could explain the differences for the abundance of predators in ground cover.

On the other hand, the adjacent vegetation showed the highest abundance of omnivores, which are mainly represented by the ant family Formicidae. It has been suggested that the formicids which inhabit olive orchards (mainly in Spain) are facultatively predatory, although some genera are mainly granivorous (Redolfi et al., 1999). In this case, such features may drive formicids to establish their colonies in adjacent vegetation, due to the availability of potential sources of food. The tendency of our results, which point out the preference of formicids for adjacent vegetation rather than olive trees, may explain the non-conclusive patterns for the abundance of ants within olive orchards shown in a previous study (Paredes et al., 2013a).

#### 4.3. Movement of natural enemies

How arthropod presence and abundance interact with the type of vegetation is an issue to consider. Overall, the patterns of movement appear to be related with the (life-cycle) developmental requirements of each guild of natural enemies. Predators and parasitoids are the guilds that moved the most between the types of vegetation (Fig. 6). From May to July the predators moved mainly from ground cover to adjacent vegetation, but also to the olive trees. This movement is related with the abundance of the neutral arthropods (Fig. 5). There is evidence that the predator *Anthrenus nemoralis* and some chrysopids showed this movement in olive orchards (Plata et al., 2017; Porcel et al., 2017). This pattern suggests that some neutral arthropods may be acting as an alternative source of food for predator insects, thus maintaining the predator population when pests are not available in the olive orchard (Chang and Kareiva, 1999; Ives et al., 2005). This is supported by the tendencies in the abundance of predators (such as Miridae) and phytophagous (such as Thripidae and Fulgoromorpha) shown in our analysis (Fig. 4).

On the other hand, from May to June, but mostly in June, parasitoids moved from ground cover to olive trees, which corresponds with the time that *P. oleae* lay their eggs on young olive fruits (Ramos et al., 1978; 1987) but also when the ground cover starts to wither. This pattern is possibly a consequence of the movement of the specialist parasitoids of olive pests, whose abundance is boosted by ground cover (Rodríguez et al., 2012; Villa et al., 2016).

In July, the omnivores moved from adjacent vegetation to ground cover and the olive trees (Fig. 6). Omnivores are mainly represented here by formicid ants, so this tendency could be a consequence of the large range of movement that formicids may present when searching for food (Plowes et al., 2013) within the olive orchard (Redolfi et al., 1999). Moreover, the movement mainly happened when the ground cover withered (Fig. 5), which may be an effect generated by the resources produced by herbaceous plants. For example, granivorous ants such as *Messor*, tend to put their nests inside the olive orchard and form big paths spreading for great distances. Conversely, facultatively predator ants such as *Tapinoma* and *Crematogaster*, can feed primarily on the honeydew of herbaceous plants but when the abundance of a pest increases they turn to feeding on such a source of food (Cerdá et al., 1989) moving towards it. This pattern increases the role of formicids to control pests within the olive trees, which can be boosted by the nearness of the adjacent vegetation (edge effects). However, this tendency needs to be investigated more thoroughly.

#### 4.4. Resource availability

A resource availability and distribution mechanism provided by the resource-based model (Ries and Sisk, 2004; Ries et al., 2004) including edge effects (López-Barrera et al., 2007; Malanson et al., 2006; Laurance, 2007; Broadbent et al., 2008) and perturbation gradients (Colwell et al., 2004; Hogsden and Hutchinson, 2004; Dallimer et al., 2012), provides a framework with which it is possible to explain the trend of our results. For example, resource distribution refers to a scenario where two adjacent habitats have different resource availability (quantity and quality). When these habitats are significantly different (high and low quality) a complementary resource distribution will drive a positive response, i.e., the low-quality habitat will have a lesser abundance of natural enemies than the other whilst the natural enemies living at the boundaries will have the advantage to boost their populations due to new resources. The resource-based model also shows that resources could be concentrated at an edge, hence increasing the abundance of natural enemies in that edge. In this context, if we consider the ground cover not only as a single habitat but also as an ecotone, we can establish that the features of the most complex study areas

in our analysis (PI-1 and PI-2) match model predictions. Conversely, when the resource availability is relatively equal in two different habitats, the abundance will be the same in both habitats, i.e., the response is neutral, which is the case of the less-complex study areas in our analysis (PI-3 and DEI). It is important to point out that changes in availability of resources may affect the multitrophic interactions in the food web, resulting in intra-guild predation between natural enemies (Tscharntke et al., 2016; Morente et al., 2018), which is a topic that needs to be investigated more thoroughly.

#### 5. Conclusions

Our findings show the importance of the presence of ground cover and adjacent vegetation in organic olive orchards. Different plant species contribute to the establishment of different guilds of natural enemies. Accordingly, our data support the complex-habitat hypothesis in organic olive orchards. When both ground cover and adjacent vegetation are maintained (functioning as a sink for natural enemies), they produce a complementary distribution of resources that needs to be maximised by high levels of complexity in order to increase the abundance of natural enemies in the orchard. To the best of our knowledge this is the first time that this type of empirical data has been recorded for organic olive orchards. Further research is needed to investigate the efficiency of this type of arrangement and the effects of habitat complexity on pest predation in organic olive orchards.

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#### Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.agee.2019.106618>.

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